The axes of interspecific interactions

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From time immemorial‘[1] species have interacted. One species might have stolen another’s food, or eaten some or part of the other species, or found a way to make a living on or inside the other one. Or perhaps they helped each other, directly or indirectly. And often, one would assume, they mostly ignored each other. Or, for a visceral introduction, see any nature documentary. Species interact, often, in myriad ways.

[1] How’s that for a first line?

My purpose, here, is to bring some clarity to these _inter_specific interactions, to provide some axes along which to sort these interactions, if not to provide clear-cut bins in which every interaction can comfortably fit. So let’s start at the beginning.

The *matrix* of interactions

Probably the simplest way to organize interspecific interactions is to consider the effect of the interaction on both players[2]. These can either be positive (+), neutral (0), or negative (-) for each player. We can place these in a matrix, of sorts, where the columns represents the effects of the interaction on species A and the rows the effects on species B (Table 1).

[2] By “effect” we ultimately mean the effect on an individual’s fitness, but usually we just mean something like the effect on growth or survival or reproduction, or even energetic reserves or something else we can easily measure.

Table 1: The classic table of interspecific interactions.

	-	0	+
+	pred/herb/parasit	commensalism	mutualism
0	amensalism	neutralism	commensalism
-	competition	amensalism	pred/herb/parasit

I'm guessing you've seen most of these labels, although amensalisms are not often considered. So easy-peasy, right?

Axes of interactions

Not so fast! While we often see the range of interspecific interactions in the form of a nice, neat table, the effects of the interactions on each player are much more accurately thought of as *continuous*. For instance, one interaction might be *slightly* negative, bordering on neutral, while anothr might be strongly negative. Are those equivalent? Probably not. So instead of thinking of interactions as falling into one of these bins in the table, imagine them as occurring along axes of interaction strengths[3] representing the effect on each of the two interacting species (Figure 1).

[3] The actual numbers in the plot do not mean much… just the sign and magnitude.

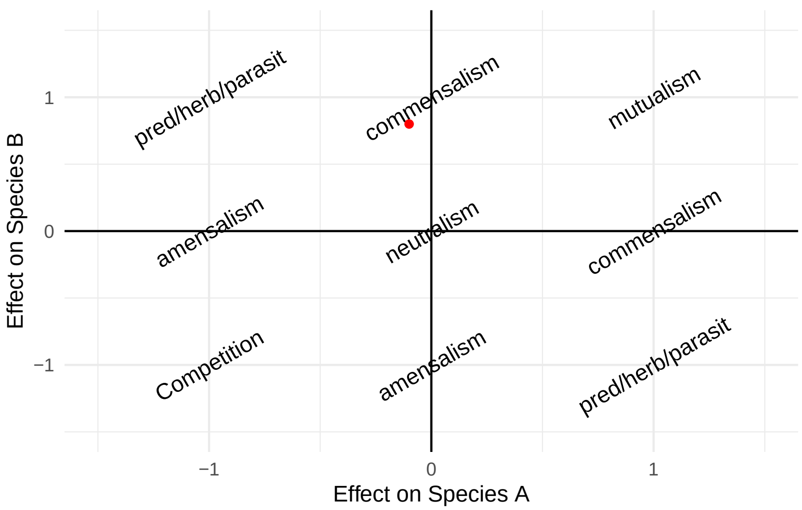

Figure 1: The axes of interactions

You will see the same labels, but the boundaries between them are intentionally vague. For instance, imagine that the red dot on the graph represents the interaction between a skin bacterium and its vertebrate host. Should we call it a parasitic interaction since Species B (the bacterium) gains a lot at the cost of Species A (the host), or a commensalism, since the effect on species A is negligible? Nature doesn't care how we label it; the important part is the impact on each species.

Many interactions means muddled categorization

Another key problem with our nice, neat categorization is that a particular interaction can exist at multiple places on the axes at the same time![4] Let's make our example (the red dot, in Figure 1) more specific. *Staphylococcus aureus* is a common and normal part of our skin and even gut microbiota. Our interaction with *S. aureus* is rather like the dot I drew on the graph, above. Except *S. aureus* is *also* known for causing horrendous skin infections, blood and bone infections, and food poisoning which are collectively linked to tens of thousands of deaths a year in the U.S.A. So…is it a parasite or commensal? Whatever we call it, we can represent the interactions between *S. aureus* and its hosts as a smear of points on the axes, from closer to commensal to more parasitic (Figure 2).

[4] In part, because while we are considering just two species, there are many individuals of each species that interact.

Symbioses are fluid

Why does this normal, largely benign commensal-ish bacterium occasionally kill people? The short answer is that context matters. Yes, there are more virulent types that have in one way or another picked up the genetic capacity to secrete enzymes, toxins, and so on that can turn them from potentially harmful to outright dangerous[5]. But more broadly, *S. aureus* tends to be an opportunistic infection.

[5] Bacteria are famously, ah…permissive of sharing mobile genetic elements, recombination, and so on.

These bacteria happily make a living on the skin of many people, primarily digesting dead skin and whatever else is available.

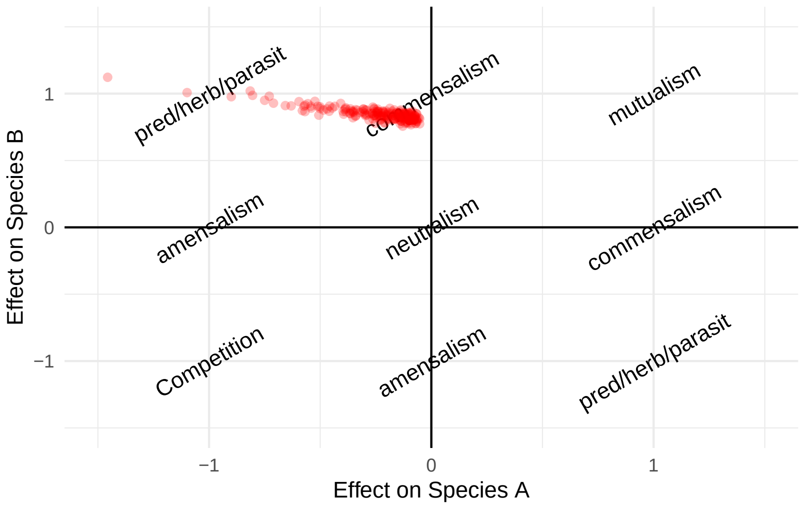

Figure 2: A more realistic sort of interaction

However, given the opportunity it may well enter a wound in the skin and start to grow; it's a nice warm, wet, nutrient rich environment, after all! It hasn't changed, but the nature of the relationships has; you now have a pus-filled wound[6]. And if the host's immune system is unable to control *S. aureus*'s growth, well that's a problem.

[6] The pus is mostly white blood cells attacking the bacteria.

Similarly, *Candidia albicans* is a normally commensal yeast found in the gut flora of roughly half of human adults, but is also an important cause of vaginal yeast infections and thrush. It can even cause systemic infections. Under what conditions do we tend to see these more problematic *Candidia* infections? In the very young, the very old, and the otherwise immunocompromised (e.g., those undergoing chemotherapy, AIDS patients).

Yes, both examples are opportunistic parasites, but the same context dependence is also common in obligate parasites. SARS-CoV-2, for instance, is well known to cause infections that vary from barely noticeable to quite deadly, and at least some of that variation is attributable context including "pre-existing conditions."

Even mutalisms can turn sour. Just like when a friend overstays their welcome, seemingly mutualistic interactions can become commensal or even parasitic given the right setting. One cool example comes from mycorrhizal fungi who typically provide hard-to-get nutrients, such as phosphorus, to their hosts plants, who in return provide sugars. What happens if you fertilize the plant with phosphorus? It stops giving the myrorrhizae sugars and may even kick them out[7]. What were once key business partners suddenly became free-loading parasites!

[7] (See, for instance, Kiers et al. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880-882.)

Many things can push a relatively benign symbiosis towards a more parasitic interaction (or vice versa). Temperature can be very important for microbial symbioses in ectotherms. Nutrient and energetic status of the host is often important, too. Dose and immune status (think immunocompromised vs. tolerant hosts) and the presence of other organisms can all change the nature of a symbiotic relationship. We will discuss some of these factors, but honestly, the range of important factors span the whole of immunology and physiology and nutrition and ecology. Suffice to say, what may clearly be a parasite in one context may be a commensal or even a mutualist in another.

Other dimentions

We define interspecific interactions in all sorts of ways beyond just their relative influence on the two players. It can be handy to spell these out.

Closeness or duration of the interaction

You have probably learned about "symbioses"[8]. The term symbiosis is Latin derived from the Greek sumbiōsis 'a living together', which is derived from from sumbios or 'companion'. In English, symbiosis means two different organisms living in close physical proximity for long periods. Often one player is larger and plays host to the other, which is often called a symbiont. So while an epiphyte[9] growing on a host tree might be considered a symbiont the same way that rhizobial bacteria are, since they are much closer to the same size this designation is rarely used. Lastly, while the relationship is often thought of as mutually advantageous, it need not be the case. So most parasitisms would be symbioses, predation and herbivory usually would not.

[8] And probably equated them, wrongly, with mutualisms.

[9] A plant growing on another plant.

Parts or wholes, one vs. many

Notice that we have lumped predation, herbivory, and parasitism all together on the axes above based on the effects the two players have on each other. But this seems a bit wrong, doesn't it? Indeed, you probably have a strong gut feeling that they are not, in fact, the same, but perhaps lack the words to explain *why* they are different. First, we can contrast predation and herbivory pretty easily, without even needing to invoke the plant vs. animal distinction. Predators kill the whole organism and then eat some or all of it[10] while herbivores eat *part* of the organism, but do not necessarily kill it[11]. Of course parasites eat parts of their hosts and do not necessarily kill it, so by this definition are they herbivores? Not if we throw in the second distinction. Parasites tend to be much smaller than their hosts and often *many* will infect (and eat) one single host. Contrast that with herbivores and predators, who are closer to the size of or larger than what they eat and where one individual will consume (parts of) many hosts.

[10] OK, sometimes the order is reversed.

[11] It helps that plants are modular, so eating a leaf or branch is much less damaging to the whole than, say, eating the leg off an antelope.

Can you think of exceptions to these distinctions? Yes, of course! We are, once again, trying to organize our thinking by placing nature on particular axes. But of course, nature doesn't care. There are all sorts of gray areas. My goal is not that you can now place every interspecific interaction neatly into categories, but that you start to think about the axes of these interactions that help us understand them better.